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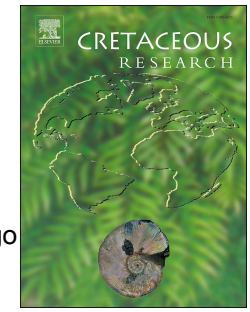

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A new late Aptian elasmosaurid from the Paja Formation, Villa de Leiva, Colombia

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Declaration of interest: none

Abstract: A new genus and species of elasmosaurid, *Leivanectes bernardoi* gen. et sp. nov., from the upper Aptian levels of the Paja Formation of Villa de Leiva (Boyacá, Colombia) is described. The new elasmosaurid is characterized by a short mandibular symphysis, bears only three alveoli (there are five in *Callawayasaurus colombiensis*), has an enlarged premaxillary alveoli, and has a mandible that includes only seven alveoli in each ramus anterior to the orbit (there are 11 in *Callawayasaurus colombiensis*). This new elasmosaurid taxon has fewer and larger alveoli than any other presently described

elasmosaurid taxon. The observed differences indicate that the new species consumed larger-bodied prey than did other elasmosaurids. The new taxon suggests that the elasmosaurids were diverse in the Colombian late Aptian sea.

Key words: Plesiosauria, Elasmosauridae, Lower Cretaceous, Aptian, Villa de Leiva, Colombia.

1. INTRODUCTION

Colombia is one of the richest South American countries in Lower Cretaceous marine reptiles. This richness is not only evident in their taxonomic diversity but also in the quantity and quality of the specimens (Páramo-Fonseca, 2015). The records are mainly concentrated in the Lower Cretaceous beds of the Villa de Leiva area (Boyacá-central Colombia), where three-dimensionally preserved and often articulated remains of plesiosaurians, ichthyosaurians and sea turtles are present (Gómez-Pérez and Nòe, 2017; Maxwell et al., 2015; Páramo-Fonseca, 2015; Páramo-Fonseca et al., 2016). The stratigraphic horizons in which these specimens are found are the Barremian and upper Aptian units of the Paja Formation, which are informally referred to as “nivel de arcillolitas abigarradas” (Etayo-Serna, 1968; Forero and Sarmiento, 1985). In addition to the exceptional preservation of most specimens, the successful preparation of many specimens by means of chemical and manual techniques (Padilla et al., 2010) allow for more detailed anatomical studies.

The plesiosaurs from Villa de Leiva are represented mainly by pliosaurids; however, some remains of elasmosaurids have also been found (Páramo-Fonseca, 2015). Welles (1962)

described and named the first elasmosaurid from northern South America, which was found in Villa de Leiva, was "*Alzadasaurus" colombiensis*, which subsequently was established as a distinct genus, *Callawayasaurus colombiensis*, by Carpenter (1999). Fragments of a skull and a mandible of a second elasmosaurid were also referred to as "*Alzadasaurus" colombiensis* (Goñi and Gasparini,1983; these remains are currently under review by MEP-F). A new elasmosaurid specimen (FCG-CBP-22) from Villa de Leiva was recently prepared and is the subject of this study. It was donated by Mr. José Sierra to the Fundación Colombiana de Geobiología in 1999 and is housed in the collections of the Centro de Investigaciones Paleontológicas in Villa de Leiva.

Specimen FCG-CBP-22 comprises the anterior section of a skull, with the jaws preserved in occlusion. It was collected from Loma La Cabrera, approximately 4 km west of Villa de Leiva. The exact location of the discovery site is not known; however, specimen FCG-CBP-22 was recovered from beds of the "nivel de arcillolitas abigarradas" of the Paja Formation. A small ammonite conch (FCG-CBP-46) was found in the surrounding matrix (Fig. 1C). The phase of tubercles development in this ammonite is comparable to that which was observed in smaller individuals (up to 35 mm diameter) of *Cheloniceras* (*Epicheloniceras*) *carlosacostai* Etayo-Serna, 1979 (cf. Etayo-Serna, 1979, pag. 34), which characterize the upper Aptian in Colombia (Etayo-Serna, pers. comm.).

2. METHODS

Specimen FCG-CBP-22 was prepared by one of the authors (MLPR), using mechanical and chemical techniques. To maintain the integrity of the fossil, a special treatment was

implemented to eliminate acidic and saline residues after acid preparation. The chemical procedure included immersions in 2% sulfamic acid followed by washes under running water for two days and submersion of the fossil into deionized water in a hermetic container. This process was repeated until a stable pH measurement was obtained. A detailed description of the method is found in Padilla et al. (2010).

The new specimen FCG-CBP-22 is an incomplete skull with the mandible preserved in occlusion. Because of its distinctively large alveoli, a comparison with other elasmosaurids focused on mesodistal measurements of alveolar size. The nomenclature used for alveoli measurements follows that of Smith and Dodson (2003: fig. 7).

FCG-CBP-22 was added to the Plesiosauria data set of O'Gorman and Coria (2016), which is based on that of O'Gorman (2016a), which in turn is based on Benson and Druckenmiller (2014). The character states of the new specimen are shown in Appendix I. Four OTUs were also incorporated to the data set: *Eromangasaurus australis* (Sachs, 2005), *Zarafasaurus oceanis* Vincent, Bardet, Pereda Suberbiola, Bouya, 2011, and *Nakonanectes bradti* Serratos, Druckenmiller and Benson, 2017, following the scoring of Serratos et al. (2017: supplemental data), and *Lagenanectes richterae* Sachs, Hornung and Kear, 2017, following the scoring of Sachs et al. (2017: supplemental data). The scoring of *Styxosaurus snowii* (Williston, 1890) was modified according to Sachs et al. (2018: appendix). Mesquite Software (Maddison and Maddison, 2011) was used to compile the new data, which comprises 95 OTUs and 276 characters, from which the phylogenetic analysis was carried out. All characters were considered to be unordered. The cladistic analysis was run on TNT (v1.5) (Goloboff and Catalano, 2016). A heuristic search with the TBR algorithm (tree bisection reconnection) recovering 20,000 trees was performed. An initial exploration for a

search of the shortest trees islands used Wegner trees (1000 random-addition sequence replicates, 1000 saved trees per replication and three random seeds). The resulting subset of most parsimonious trees (MPTs) was used as the initial group of trees for a TBR search. A strict consensus was applied, and the IterPCR algorithm was run to determine and prune the unstable OTUs in the consensus (Pol and Escapa, 2009). The consistency (CI) and retention (RI) indexes (Farris, 1989) were calculated, and Bremer support values (Bremer 1994) were computed for some nodes in the reduced consensus cladogram.

2.1 Institutional Abbreviations

BGR, Bundesanstalt für Geowissenschaften und Rohstoffe, Hannover, Germany; **FCG-CBP**, Fundación Colombiana de Geobiología, Centro de Investigaciones Paleontológicas; **ICNMHN**, Instituto de Ciencias Naturales, Universidad de Colombia, Bogotá, Colombia; **KUVP**, Kansas University, Vertebrate Paleontology, United States; **NPC**, National Paleontological Collection, Lower Hutt, New Zealand; **NSM**, National Science Museum, Tokyo, Japan; **OCP**, Office Chérifien des Phosphates, Khouribga, Morocco; **QM**, Queensland Museum, Brisbane, Australia; **RSM**, Royal Saskatchewan Museum, Regina, Saskatchewan, Canada; **SMUSMP** Southern Methodist University, Shuler Museum of Paleontology, Dallas, USA; **UCPM**, University of California Museum of Paleontology, California, USA; **UNSM**, University of Nebraska State Museum, Lincoln, USA.

2.2 Unique digital ZooBank registration identifier:

3. SYSTEMATIC PALEONTOLOGY

SAUROPTERYGIA Owen, 1860

PLESIOSAURIA de Blainville, 1835

PLESIOSAUROIDEA Welles, 1943

ELASMOSAURIDAE Cope, 1869

Leivanectes gen. nov.

LSID:

Type and only species: *Leivanectes bernardoi* sp. nov.

Diagnosis: For type and only known species.

Derivation of name: From Villa de Leiva, which is the locality where the holotype was collected, and Greek *nektos*, swimmer.

Leivanectes bernardoi sp. nov.

LSID:

Holotype: FCG-CBP-22. Anterior half of the skull comprising the rostrum, part of the orbital area and anterior half of the mandible.

Type locality and horizon: Loma La Cabrera, Villa de Leiva, Department of Boyacá, central Colombia. Upper section of the "nivel de arcillolitas abigarradas" of the Paja Formation (Etayo-Serna, 1968), upper Aptian (Etayo-Serna, pers. comm.) (Fig. 1).

Derivation of name: In honor of Dr. Carlos Bernardo Padilla, who is recently deceased and who dedicated part of his life to the rescue and preservation of fossils mainly from the area of Villa de Leiva. Dr. Carlos Bernardo Padilla is the founder, along with his brother

Santiago Padilla, of the prestigious Centro de Investigaciones Paleontológicas in the town of Villa of Leiva, Colombia.

Differential diagnosis: Elasmosaurid with the following combination of features: premaxilla without dorsal medial ridge, differing from *Callawayasaurus colombiensis*, *Eromangasaurus australis,* and Late Cretaceous elasmosaurids; meso-distal measurement of the third and fourth premaxillary alveoli approximately 14% of the preorbital length, differing from the smaller alveoli that was recorded for *Callawayasaurus colombiensis, Tuarangisaurus keyesi* and aristonectines; three alveoli pairs adjacent to the mandibular symphysis, a feature shared with *Terminonatator ponteixensis*; five premaxillary alveoli, which differs from that of *Elasmosaurus platyurus* (6+) and *Eromangasaurus australis* (3-4); vomers lacking a posterior medial V-shaped notch near the internal nares to accommodate the pterygoids, which differs from that of *Lagenanectes richterae* and *Morturneria seymourensis*; seven mandibular alveoli anterior to the orbit, which differs from *Callawayasaurus colombiensis* (~11), *Futabasaurus suzukii* (~12), *Libonectes morgani* (~10), *Styxosaurus* spp (9+), *Terminonatator ponteixensis* (~10), *Thalassomedon haningtoni* (~10), and *Tuarangisaurus keyesi* (~10); absence of a dentary ventral elaboration along the mandibular symphysis, which differs from that of *Callawayasaurus colombiensis*, *Eromangasaurus australis*, *Lagenanectes richterae* and *Zarafasaurus oceanis*; and elliptical external nares, which differs from the cordate external nares of *Nakonanectes bradti*.

4. DESCRIPTION

156 **4.1 Cranium**

157 FCG-CBP-22 is an incomplete skull with its mandible preserved in occlusion. The most
158 anterior part of the specimen including the rostrum and mandibular symphysis is well
159 preserved and undeformed. The interorbital part of the skull roof is dorsoventrally crushed
160 (Fig. 2).

161 **Premaxilla**: Both premaxillae are well preserved and form almost the entire rostrum. The
162 rostrum is wide and dorsally convex in the cross section. The premaxilla lacks a medial
163 ridge, as it does in *Futabasaurus suzukii* Sato, Hasegawa and Manabe, 2006, *L. richterae*
164 and basal plesiosauroids (Benson and Druckenmiller, 2014; Sachs et al., 2017; Sato et al.,
165 2006; Serratos el al., 2017). The midline suture is visible along the entire premaxillary
166 length, with the exception of its anteriormost tip. The premaxilla forms the anterior and
167 medial margin of the external naris (Fig. 2). Each premaxilla bears five alveoli that create a
168 slightly waved margin in a lateral view. A change in the alveoli size is observed at the
169 premaxilla-maxilla contact, but there is no diastema (Fig. 2B). The dorsomedial process of
170 the premaxilla is progressively higher toward the internarial sector (Fig. 2C). The
171 dorsomedial process is broken at the level of the anterior border of the orbit and appears to
172 be projected over the frontals; however, its posterior extension remains unknown. The
173 dorsal surface of the premaxilla is slightly wrinkled and bears a neurovascular foramina
174 that are randomly distributed, three of which are larger and aligned near the midline.

175 **Maxilla:** The premaxilla-maxilla suture is slightly curved along its length. The maxillae
176 form the ventral margin of the external nares and the anterolateral margin of the orbit (Fig.
177 2C). In the lateral view, the alveolar border of the maxilla shows a slight ventrally convex

curve that includes the 1st to the 4th alveoli. Although incomplete, the left maxilla bears nine alveoli. In the palatal view, the anterior part of the maxillae is not well exposed, but its contact with the vomers is insinuated. The maxilla-palatine junction is barely visible on both sides of the skull, and it begins at the posterior rim of the internal naris. The maxilla forms the lateral margin of the internal naris (Fig. 2D).

External naris: Both external nares are poorly preserved along the posterior border (Fig. 2C). The external naris is located at the level of the second maxillary alveolus. The distance from the external naris to the midline of the skull is equivalent to the width of the external naris, which is shorter than that of *F. suzukii* and *N. bradti* (Sato et al., 2006; Serratos et al., 2017). The distance from the external naris to the orbit is as short as it is in *Callawayasaurus colombiensis* (Welles, 1962) and in *E. australis* (Kear, 2005: fig. 6; Sachs, 2005a: fig. 3A; Welles, 1962: fig. 3) and is shorter than that in *F. suzukii* (Sato et al., 2006). The participation of the frontal in the narial margins cannot be established due to the poor preservation of this area.

Orbit: Both orbits are incomplete. Their posterior region is missing. The preserved orbital areas are slightly expanded laterally (Fig. 2C). The presence of a dorsally convex ventral margin of the orbit, a feature that is common among elasmosaurids (Benson and Druckenmiller, 2014; Carpenter, 1999), cannot be established due to the poor preservation of this margin.

Frontal: Both frontals are partially crushed and, therefore, an accurate description of these bones cannot be given. The frontal forms an expanded table over the orbits, as in *C. colombiensis* (Welles, 1962), but its relationship with the dorsomedial process of the

200 premaxilla remains unclear. The right frontal contacts posteriorly a small preserved portion
201 of the parietal (Fig. 2C).

202 **Prefrontal**: A fragment of each prefrontal is exposed on both sides of the skull. Both
203 prefrontals are broken and are slightly displaced from their anatomical place. The prefrontal
204 forms part of the anterior margin of the orbit (Fig. 2C), as in *N. bradti* (Serratos et al.,
205 2017). Their poor preservation prevents the establishment of the shape and extension of this
206 element**.**

207 **Postfrontal**: The postfrontals are only represented by two small bone fragments that are
208 badly preserved on the posterior region of the orbits (Figs. 2B, C).

209 **4.2 Palate**

210 The palate is incomplete and is partially covered by the mandibular rami. It preserves the
211 anterior process of the pterygoids, the anterior part of the palatines and the posterior portion
212 of the vomers.

213 **Vomer**: The anterior end of the vomers is not visible, because the mandible is in occlusion.
214 Both vomers are united, but they are not completely fused along the midline. In its middle
215 region, the vomer is narrow and forms the medial margin of the internal naris. The vomer
216 extends posterior to the internal naris, as is common in elasmosaurids (Carpenter, 1997: fig.
217 2D; O'Gorman et al., 2017: fig. 7B; O'Keefe, et al., 2017: fig. 4C; Sato et al., 2006: fig. 4C;
218 Vincent et al., 2011: fig. 2D, E; Welles, 1962: fig. 4A). The posterior region of the vomer is
219 limited laterally, with the palatine through an irregular suture, and medially with the
220 anterior margin of the pterygoid. The vomers are not separated by the pterygoids along the

midline (Fig. 2D), which is a condition that is also seen in *F. Suzukii*, *Libonectes morgani* (Welles, 1949) and *Z. oceanis* (Sato et al., 2006; Vincent et al., 2011; Welles, 1949: Plate 3).

Palatine: Both palatines are incomplete. The preserved portion of each palatine is a flat to slightly convex plate that medially contacts the pterygoid and the vomer (Fig. 2D). Although the suture with the maxilla is not clear on either side, the anterior end of the palatine narrows and appears to form the posterior border of the internal naris, which is known in other elasmosaurids (Carpenter, 1997: fig. 2D; O'Gorman et al., 2017: fig. 7B; Sachs et al., 2017: fig. 3; Sato et al., 2006: fig. 4C; Vincent et al., 2011: fig. 2D, E; Welles, 1962: fig. 4A).

Pterygoid: Only the anterior process of the pterygoid is preserved. The pterygoid medially joins its counterpart, anteriorly joins the vomer and laterally joins the palatine. In the ventral view, the pterygoids form a concave area between the palatines. However, this appears to be a taphonomic feature (Fig. 2D).

Internal naris: The internal naris is not entirely distinguishable. It is approximately 20 mm in length and 8 mm in width. Each internal naris is limited by the maxilla, the vomer and probably the palatine to a limited extend (Fig. 2D).

4.3 Mandible

Dentary: The dentaries are fused along the mid-line of the symphysis (Fig. 2C) and, because the mandible is in occlusion, it is difficult to see if this fusion is also complete on the dorsal surface of the symphysis. In the ventral view, the external surface of dentaries is

marked by a great quantity of pits at the symphyseal region, which differs from the less densely distributed pits that cover the external surface of each mandibular ramus (Figs. 2A, B, D). The ventral surface of the dentaries along the mandibular symphysis lacks any elaboration (Figs. 4C, E), such as in. *L. morgani* and *N. bradti* (Serratos et al., 2017; Welles, 1949), and differs from *E. australis*, *L. morgani* and *S. snowii*, in which a symphyseal keel is observed (Kear, 2007; Sachs and Kear, 2017; Sachs et al., 2018: fig. 3B). In the lateral view, the symphysis includes only three pairs of large alveoli for functional teeth, as in *Terminonatator ponteixensis* Sato 2003, *S. snowii* and *N. bradti* (Sachs et al., 2018; Sato, 2003; Serratos et al., 2017). In the anterior view, there are two pairs of alveoli that are anteriorly directed, which is similar to the premaxillae (Fig. 2A).

Angular: The anterior end of both angulars is preserved. In the ventral view, the angular is exhibited posterior to the level of the internal nares (Fig. 2D) but less posterior than in *T. ponteixensis* or *N. bradti* (Sato, 2003; Serratos et al., 2017). In the medial view, the anterior end of the angular forms a wedge that anteriorly tapers against the splenial, posterior to the mandibular symphysis.

Splenial: The preserved portion of the splenials forms a long and narrow blade tapering anteriorly. The splenials end where the symphysis begins, as in *L. morgani* (Welles, 1949).

Coronoid: The coronoid forms the dorsal half of the medial wall of the preserved part of the mandible and extends anteriorly to approximately 2 cm posterior to the symphysis, as in *L. morgani* (Welles, 1949). The anterior end of the coronoid contacts the dentary in an S-shaped suture.

4.4 Alveoli and dentition

The alveoli of the upper jaw differ in size. Their mesodistal measurements are shown in Table 1. The first premaxillary alveolus is procumbent and small but is not significantly smaller than the second. However, its diameter is less than half that of the third alveolus (Table 1). This condition is found in *L. richterae* (Sachs et al., 2017), *S. snowii* (Sachs et al., 2018: Appendix) and *T. ponteixensis* (Sato, 2003). The third alveolus is the largest and is similar to the fourth, while the fifth is smaller. The more complete left maxilla bears nine alveoli and, extrapolating the possible length of the missing part, and it is probable the total number of alveoli was approximately eleven. The alveoli of this maxilla are of different sizes, which indicates a heterodont dentition. The first is relatively small compared with the others that are variable in size (see Table 1). There are twelve alveoli in the left mandibular ramus and eleven on the right. The seven anterior alveoli are similar in size and those that are more posterior are smaller.

Twelve fragmentary teeth are preserved, seven of which are almost complete and five that are broken at their crown base. The surfaces of the teeth are damaged, and only their labial surfaces can be observed. The crown is conical in shape and circular in the cross section, as in *C. colombiensis* and *L. richterae* (Sachs et al., 2017; Welles, 1962). The surface of the enamel is practically smooth. However, on the labial side of the more complete tooth, very slight ridges and transversal wrinkles in the basal two-thirds of the crown are present (Fig. 2E), which is similar to those described by Welles (1949) for the teeth of *L. morgani*.

5. DISCUSSION

5.1 Morphological comparisons

286 The specimen FCG-CBP-22 shows well-ossified elements and some closed sutures, such as
287 the symphysis, which indicates that the individual was osteologically mature at the time of
288 death (sensu Brown, 1981).

289 Although the specimen FCG-CBP-22 is an incomplete skull and does not preserve any of
290 the autapomorphic characteristics of Elasmosauridae, some of the cranial features
291 registered as diagnostic of elasmosaurids (Brown, 1981; Ketchum and Benson, 2010;
292 O'Keeffe, 2001; Vincent et al., 2011) are present including vomer extended posterior to the
293 internal nares (O'Keefe, 2001), splenial without participation in the mandibular symphysis
294 (Ketchum and Benson, 2010) and absent of an anterior interpterygoid vacuity (Vincent et
295 al., 2011). The new specimen also presents the following two features that together indicate
296 its elasmosaurid affinities: a nonelongated rostrum and premaxilla dorsomedial process
297 projecting over the frontals. These characteristics are present in all elasmosaurids, with the
298 exception of *Callawayasaurus colombiensis*, in which the premaxilla tapers more
299 proximally (Benson and Druckenmiller, 2014; J.P.O'G Pers. Obs.).

300 The early Cretaceous elasmosaurids that can be compared with *L. bernardoi* include the
301 late Aptian *C. colombiensis* UCMP 38349 (Figs. 3C-E and 4A-D), and UCMP 125328
302 (Figs. 4E-F) from Villa de Leiva (Welles, 1962), the Albian *E. australis* from Australia
303 (Kear, 2005, 2007; Sachs, 2005a), and the late Hauterivian *L. richterae* from Germany
304 (Sachs et al., 2017). The more distinctive feature of the new taxon *L. bernardoi* is the
305 presence of large alveoli that result in a lower number of alveoli in the different regions of
306 the cranium and mandible. *L. bernardoi* has five premaxillary alveoli, which differs from
307 the maximum of four premaxillary alveoli in *E. australis*, (Kear, 2007) and the minimum of
308 six premaxillary alveoli in *Elasmosaurus platyurus* Cope, 1868 (Sachs, 2005b). In Table 2

309 the alveolar account of *L. bernardoi* (FCG-CBP-22) is contrasted with that of the Early
310 Cretaceous elasmosaurids and other comparable Late Cretaceous elasmosaurids, which
311 have 4-5 premaxillary alveoli (*F. suzuki, L. morgani, Thalassomedon haningtoni* Welles,
312 1943, *Tuarangisaurus keyesi* Wiffen and Moisley, 1986, *Z. oceanis, T. ponteixensis,*
313 *Styxosaurus browni* Welles, 1952, *S. snowii* and *N. bradti*). *L. bernardoi* have the same
314 number of alveoli pairs on the mandibular symphysis (three alveoli) as *T. ponteixensis, S.*
315 *snowii* and *N. bradti*. It has seven mandibular alveoli anterior to the orbit, while all the
316 other taxa have more than seven.

317 *L. bernardoi* is different from other elasmosaurids, except for *N. bradti*, in the ratio
318 between the mesiodistal measurements of the premaxillary alveoli and the preorbital length
319 (Figs. 3A, B). In *L. bernardoi*, the meso-distal measurement of the third and fourth
320 premaxillary alveoli is approximately 14% of the preorbital length. Although no
321 measurements were taken, this ratio seems to be similar in *N. bradti* (Serratos et al., 2017:
322 fig. 2) and different in other elasmosaurids, such as the Lower Cretaceous *C. colombiensis*
323 (~6%), *E. australis* (~8%) (Kear, 2007: fig. 1A), and *L. richterae* (~11%) (Sachs et al.,
324 2017: fig. 4); the Upper Cretaceous elasmosaurids *Z. oceanis* (~12%-~13%) (Lomax and
325 Wahl, 2013: fig Vincent et al., 2011: fig. 2), *L. morgani* (~11%) (Sachs and Kear, 2017: fig.
326 1A, C), *T. keyesi* (~10%-~8%) (O´Gorman et al., 2017: fig. 2), *T. haningtoni* (~9%)
327 (Carpenter, 1999: fig. 12), *S. snowii* (~9%) (Sachs et al., 2018: fig. 1), and *F. suzukii* (~5%)
328 (Sato et al., 2006: fig. 4); and the aristonectine elasmosaurids (~3%) (Otero et al., 2012,
329 2014), which have long skulls with an increased number of teeth.

330 There are other features that distinguish *L. bernardoi* from other comparable elasmosaurids,
331 mainly from those of the early Cretaceous, which are worth discussing. The position of the

external naris in *L. bernardoi* (at the level of the second maxillary position) differs from that in *Z. oceanis* (first maxillary position) (Lomax and Wahl, 2013: fig 5; Vincent et al., 2011: fig. 2) and those in *S. snowii*, *N. bradti* or *L. morgani* (third or posterior to the third maxillary position) (Sachs and Kear, 2017: fig. 1C; Sachs et al., 2018; Serratos et al., 2017: fig. 3). The absence of the dorsomedial ridge in the premaxillae of *L. bernardoi*, which is a characteristic that it shares with *L. richterae* and *F. Suzukii* (Sachs et al., 2017; Sato et al., 2006), differs from the keeled premaxillae that are found in most elasmosaurids, including *C. colombiensis* (Figs. 4A, B, D), *E. australis* and *N. bradti* (Benson and Druckenmiller, 2014: character 17; Kear, 2007; Serratos et al., 2017; Welles, 1943, 1962). The size and form of the external nares of *L. bernardoi* differ from the small cordate external nares of *N. bradti* (Serratos et al., 2017). In *L. bernardoi*, the palatine participates only in the posteromedial tip of the internal naris, while in *L. richterae*, the palatine forms the posterolateral margin of the internal naris (Sachs et al., 2017: figs. 3A, B). In *L. bernardoi*, the pterygoids are not visible between the vomers, while in *L. richterae* and in *M. seymourensis*, the vomer has a posterior medial V-shaped notch from which the pterygoids can be seen (Chatterjee and Small, 1989; O'Keefe et al., 2017; Sachs et al., 2017). *M. seymourensis* also has in the vomer a medial ventral ridge (O'Keefe et al., 2017) that is absent in *L. bernardoi*.

The normal ventral surface of the dentaries along the mandibular symphysis of *L. bernardoi* differs from that of *L. richterae*, which exhibits a platform (Sachs et al., 2017: fig. 7); those of *E. australis*, *Z. oceanis*, *L. morgani* and *S. snowii*, which have a symphyseal keel (Kear, 2007; Sachs and Kear, 2017; Sachs et al., 2018: fig. 3B, Vincent et al., 2011); that of *F. suzukii*, which has a symphyseal pit (Sato et al., 2006); and those of *T. keyesi* and *C.*

355 c*olombiensis*, which have a narrow symphyseal sulcus (Welles, 1962; O'Gorman et al.,
356 2017: fig. 9L). The symphyseal ventral groove, which is slightly marked in *L. bernardoi*, is
357 deep in *C. colombiensis* (Figs. 4C, E). The non-participation of the angular and splenial in
358 the mandibular symphysis distinguishes *L. bernardoi* from *S. snowii*, in which the angular
359 participates (Sachs et al., 2018), and from *N. bradti*, in which the splenial participates
360 (Serratos et al., 2017).

361 In the new specimen and in *C. colombiensis*, the first premaxillary alveolus is smaller than
362 the second and third, but the difference in size is more significant in *C. colombiensis* (Figs.
363 3D-E, H). On the other hand, in *N. bradti*, *T. keyesi* and *T. haningtoni*, the first
364 premaxillary alveolus is not significantly smaller than the third (Serratos et al., 2017;
365 Welles, 1943; Wiffen and Moisley, 1986), which differs from the condition that is found in
366 *L. bernardoi*. The alveoli of *L. bernardoi* are relatively larger than those of *C.*
367 *colombiensis*. This is evident for both, in the anterior view (Figs. 3A, B, D, E, H), and in
368 comparing the position of the tenth mandibular alveolus (Figs. 3C, F, G). This alveolus is
369 located near the middle of the orbit in *L. bernardoi* (Figs. 3F, G) but anterior to the anterior
370 margin of the orbit in the UCMP 38349 specimen of *C. colombiensis* (Fig. 3C). The
371 circular cross section of the teeth of *L. bernardoi* is shared with *L. richterae, E. australis*
372 and *C. colombiensis* (Kear, 2005; Sachs et al., 2017, Welles 1962) and differs from the
373 labiolingually compressed teeth of most of the Late Cretaceous elasmosaurids (Sachs and
374 Kear, 2017; Sachs et al., 2017; Sachs et al., 2018;Serratos et al., 2017: character 139) and
375 the “D” shaped tooth cross section of *N. bradti* (Serratos et al., 2017). The smooth texture
376 of the crown of *L. bernardoi* is similar to that of *C. colombiensis*, but in *L. bernardoi*, the
377 enamel has very slight ridges and transverse wrinkles towards the base of the crown, while

in *C. colombiensis*, it has anterior and posterior edges that are finely striated longitudinally (Welles, 1962). Transverse wrinkles, which are similar to those of *L. bernardoi*, were described for *L. morgani* (Welles, 1949), while in most elasmosaurids, the crowns show more regular longitudinal ridges (Chatterjee and Small, 1989; Sachs et al., 2017; Sato, 2003; Sato et al., 2006; Serratos et al., 2017; Vincent et al., 2011; Wiffen and Moisley, 1986).

5.2 Phylogenetic analysis

The Wagner tree search resulted in a subset of 5000 parsimonious trees (MPTs), and the final phylogenetic analysis resulted in 20000 MPTs with 1502 steps (CI=0.273 and RI= 0.667). The strict consensus (Fig. 5A) recovers *L. bernardoi* within the Elasmorauridae clade, which is identified only by postcranial synapomorphies. *L. bernardoi* is the sister taxa of *T. keyesi* and *T. haningtoni*. This node (*L. bernardoi* + (*T. keyesi* + *T. haningtoni*)) is closely related to the node *L. morgani*+ (*S. snowii* + *H. alexandrae)*, which forms a well-resolved branch. In contrast, the basal elasmosaurids, including the Early Cretaceous *C. colombiensis* and *E. australis*, as well as some Late Cretaceous elasmosaurids, were recovered within polytomies that are only resolved after pruning unstable OTUs, which were identified by applying the IterPCR algorithm (Figs. 5A-B). The elasmosaurids that were identified as unstable OTUs were *E. australis*, *C. colombiensis*, *E. platyurus* and *Z. oceanis*.

L. bernardoi is differentiated from the *T. keyesi* + *T. haningtoni* node by the absence of a dorsomedian ridge in the premaxilla (17.0), which is a characteristic that is found in

leptocleidid plesiosauroids, and by the smaller size of the first premaxillary alveolus (140.1), a characteristic also found in the closely related *L. morgani* + (*S. snowii* + *H. alexandrae*) node. *L. bernardoi* is grouped with *T. keyesi* + *T. haningtoni* and is separated from the *L. morgani* + (*S. snowii* + *H. alexandrae*) node by the reduced size of the distalmost alveolus of the premaxilla (132.1). Altogether, these taxa form a branch that can be distinguished from all of the other elasmosaurids by the posteromedian process of the premaxilla not expanding into the original width posterior to the naris (22.1), and by two postcranial synapomorphies that are unknown in *L. bernardoi*: there are more than 60 cervical vertebrae and pubis without anterolateral cornu.

5.3 Dentition differences and trophic changes

Elasmosaurids have largely been considered to be ecologically optimized to middle trophic-level aquatic predation based on the presence of narrow tooth crowns with a markedly elongated profile that indicates structural fragility (Massare, 1987; Kear et al., 2017). However, even among elasmosaurids there is a clear tooth morphological variation. Differences in related features, such as symphyseal length, number of symphyseal alveoli, tooth shape and increase in the number of alveolar count, have been observed in the Late Cretaceous aristonectines (*A. parvide*ns, *Kaiwhekea katiki* Cruickshank and Fordyce, 2002) and have been associated with differences in prey capture strategy and prey preference compared with non-aristonectines (Cruickshank and Fordyce, 2002; O'Gorman, 2016; Otero et al., 2014). Following the same argumentation line, the differences in dentition and alveoli size between *L. bernardoi* and *C. colombiensis* (the alveoli of *L. bernardoi* are

422 larger than those of *C. colombiensis*; the mandible of *L. bernardoi* shows less alveoli than
423 those observed in *C. colombiensis,* and the symphysis of *L. bernardoi* is longer and bears
424 fewer teeth) appear to indicate a subdivision in prey preference between species from the
425 similar locality and age (late Aptian). These differences suggest specialization in the
426 feeding of the Early Cretaceous Colombian elasmosaurids, with *L. bernardoi* likely being
427 able to consume prey that are larger than those preferred by *C. colombiensis*.

428 It is interesting to remark that the decrease in tooth count was achieved several times during
429 the elasmosaurid history, as is recorded in *Z. oceanis* from the Maastrichtian of Morocco
430 (Lomax and Wahl, 2013; Vincent et al., 2011). Nevertheless, in *Z. oceanis,* the reduction in
431 tooth number is associated with a decrease in alveolar size (Lomax and Wahl, 2013, fig. 7,
432 8), which is not the case in *L. bernardoi*. Therefore, differences in the teeth number and
433 proportions that are observed in Cretaceous elasmosaurids seem to indicate changes in their
434 food preferences throughout their history. The contemporaneity of *L. bernardoi* and C.
435 *colombiensis* suggests that the elasmosaurids have achieved diverse prey preferences since
436 the Early Cretaceous, at least in the Colombian sea.

437

438 **6. CONCLUSIONS**

439 The new specimen FCG-CBP-22 is defined as a new genus and species of Elasmosauridae,
440 *Leivanectes bernardoi* gen. et sp. nov., by having large premaxillary alveoli and a
441 distinctive amount of alveoli in the different regions of the cranium and mandible. *L.*
442 *bernardoi* differs from other Lower Cretaceous elasmosaurids in that it has five
443 premaxillary alveoli, three pairs of alveoli on the mandibular symphysis, seven mandibular

alveoli anterior to the orbit, the tenth mandibular alveolus located near the level of the middle of the orbit, the absence of a symphyseal ventral elaboration, and vomers that do not form a posterior medial V-shaped notch to accommodate the pterygoids. *L. bernardoi* represents the second elasmosaurid species that was defined from the Aptian of Colombia and the Lower Cretaceous of South America.

The large alveoli of *L. bernardoi* allows for a feeding habit that relies on prey of greater size than those chosen by others elasmosaurids, including *C. colombiensis*. Since both *L. bernardoi* and *C. colombiensis* come from the upper Aptian beds of the same geographic region, these differences suggest that the elasmosaurids could have attained a wide range of morphologies during the Early Cretaceous, at least in the Colombian sea.

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608

609 **APPENDIX I**

610 Character states of *Leivanectes bernardoi* gen. et sp. nov.

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617 Figure captions

618 Figure 1. Geographic and stratigraphic provenance of the holotype specimen FCG-CBP-22
619 of *Leivanectes bernardoi* gen. et sp. nov. A, locality where FCG-CBP-22 was collected
620 (arrow). B, generalized stratigraphic column of the Paja Formation showing the specimen

621 occurrence (modified from Etayo-Serna, 1979). C, lateral and ventral views of
622 *Cheloniceras* (*Epicheloniceras*) *carlosacostai* Etayo-Serna, 1979 (FCG-CBP-46) found
623 with the skeletal remains (scale bar = 5mm).
624

625 Figure 2. *Leivanectes bernardoi* gen. et sp. nov., holotype (FCG-CBP-22), A-D,
626 photographs and interpretative drawings of skull and mandible in anterior (A), left lateral
627 (B), dorsal (C) and ventral (D) views. Dashed lines: interpretative limits (Scale bar = 20
628 mm). E, photograph of the fourth right premaxillary tooth in lateral view (Scale in cm).
629 Abbreviations: **1st**, **2nd, ...,** premaxillary alveolus; **a**, angular; **c**, coronoid; **de**, dentary; **fr**,
630 frontal; **mx**, maxilla; **p**, parietal; **pl**, palatine; **pmx**, premaxilla; **pof**, postfrontal; **prf**,
631 prefrontal; **pt**, pterygoid; **sp**, splenial; **v**, vomer.
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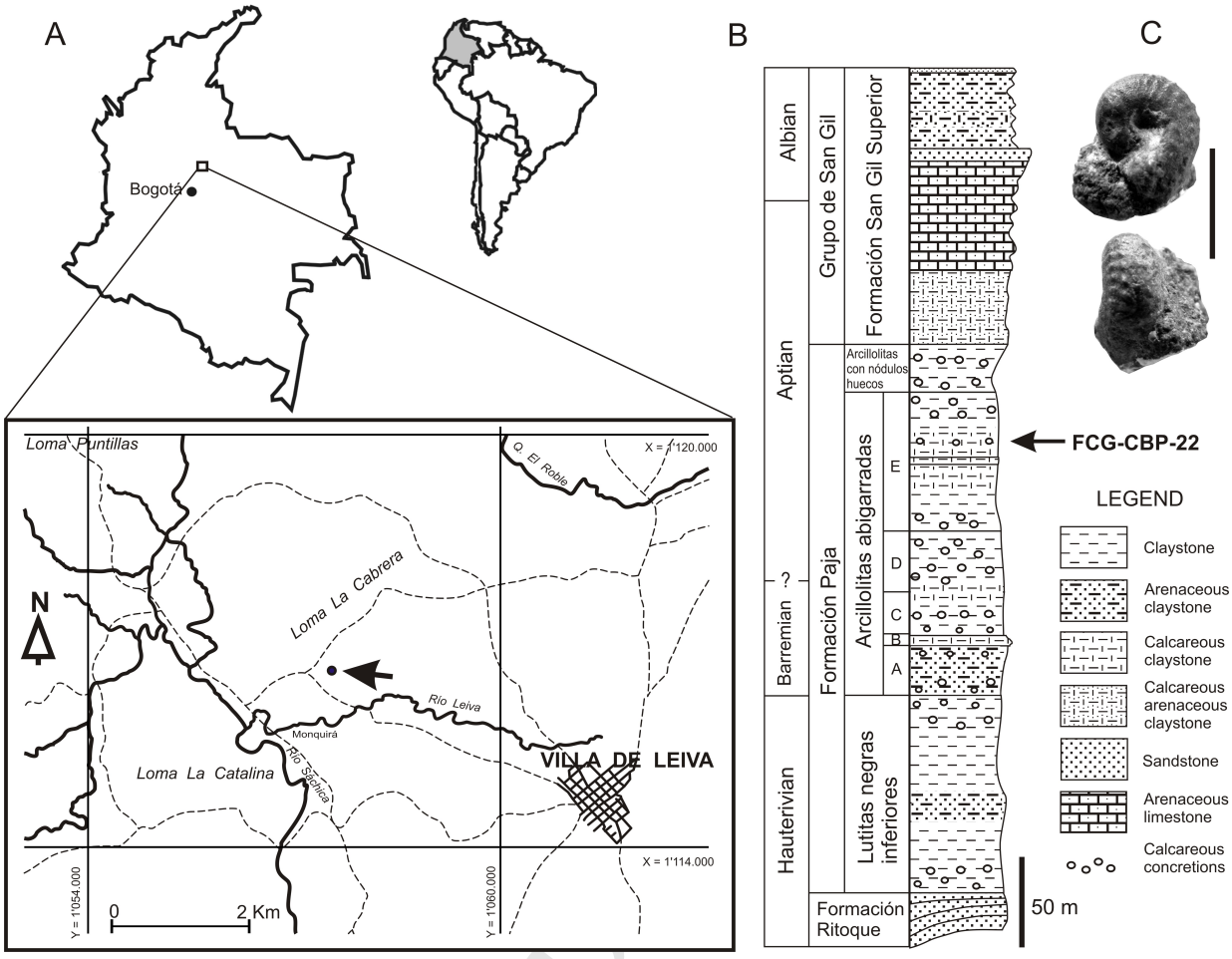
633

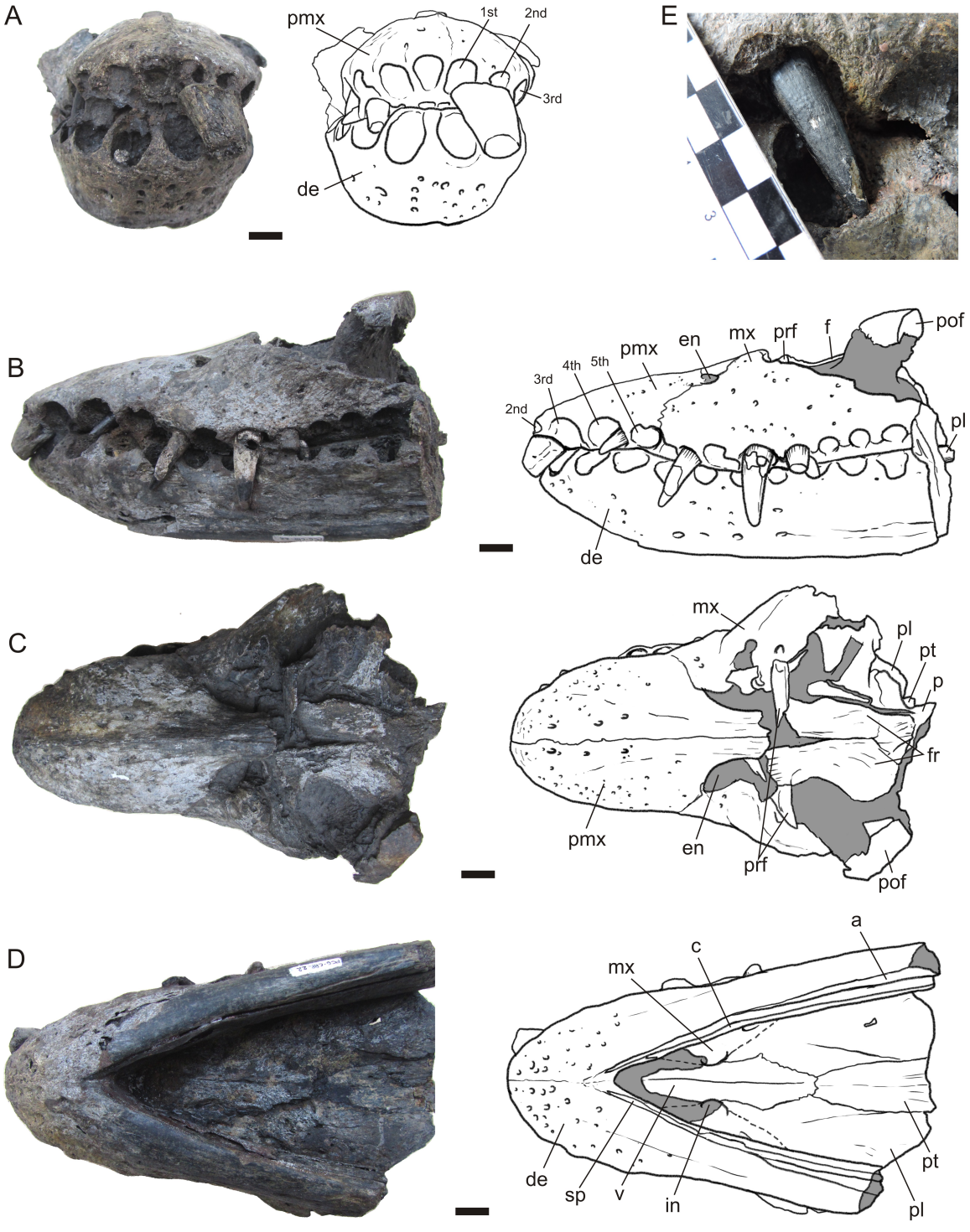
634 Figure 3. A-B, plot of mesio-distal length of premaxillary alveoli of *L. bernardoi* (FCG-
635 CBP-22), *C. colombiensis* (UCMP 125328) and *T. keyesi* (NPC CD 425),
636 100*AMD/preorbital length (A), and, absolute measures (AMD) (B). C-H, comparison of
637 alveolar features between the *C. colombiensis* holotype (UCMP 38349), referred specimen
638 (UCMP 125328) and holotype of *L.bernardoi* FCG-CBP-22. C and F, the anterior orbital
639 margin (vertical line) and the tenth mandibular alveoli (arrow) in *C. colombiensis* holotype
640 (C) and *L. bernardoi* (F, G). D, E and H, comparison of anterior views of *C. colombiensis*,
641 holotype (D) and referred specimen (E), and *L. bernardoi* (H) (Scale bars = 20mm).
642

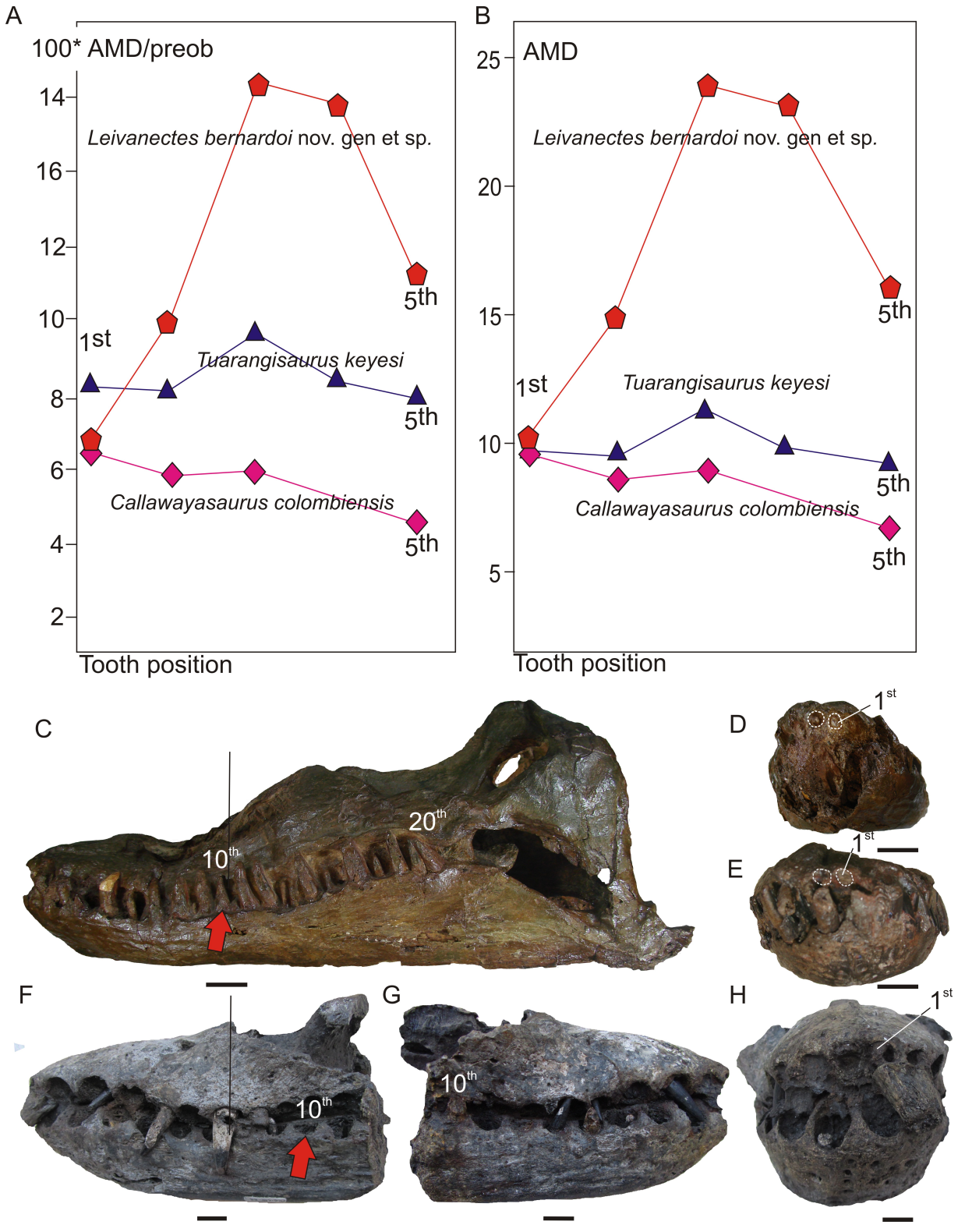
643 Figure 4. *C. colombiensis* skull and mandible. A-D, holotype (UCMP 38349) in right lateral
644 (A), left lateral (B), ventral (C) and dorsal (D) views. E-F, referred specimen (UCMP
645 125328) in ventral (E) and dorsal (F) views (Scale bars = 20 mm). Abbreviations: **pmr,**
646 premaxillary ridge; **svg,** symphyseal ventral groove.
647
648
649 Figure 5. A-B, Plesiosauroidea branch from the phylogenetic analysis of Plesiosauria data
650 set (See material and Methods). A, strict consensus of 20000 most parsimonious trees, 1502
651 steps, obtained after (TBR) branch swapping. Bremer Support indicated below some nodes.
652 B, reduced most parsimonious tree after pruning unstable taxa (Plesiosauroidea pruned
653 OTUs: *Hastanectes valdensis*, *Callawayasaurus colombiensis*, *Eromangasaurus australis*,
654 *Elasmosaurus platyurus* and *Zarafasaura oceanis*).
655
656 Table 1. Mesodistal measurements of the premaxillary and maxillary alveoli (in mm). The
657 maxillary alveoli measurements were taken from the left side of the skull.
658
659 Table 2. Alveolar account of several elasmosaurids (data Taken from Carpenter, 1997: fig.
660 2; Kear, 2005, 2007; Lomax and Wahl, 2013; O'Gorman et al., 2017: fig. 7A, B, 9M; Otero,
661 2016; Sachs et al., 2017; Sachs et al., 2018: fig. 1B; Sato, 2003: fig. 5; Sato et al., 2006: fig.
662 4A; Serratos et al., 2017: fig. 3, 4; Vincent et al., 2011: fig. 4A;; Welles, 1943, 1949, 1962;
663 J.P.O'G pers. obs.).

Premaxillary alveolus	Mesodistal measurement	Maxillary alveolus	Mesodistal measurement	Maxillary alveolus	Mesodistal measurement
1st	10	1st	9	6th	18
2nd	15	2nd	14	7th	13
3rd	24	3rd	20	8th	11
4th	23	4th	21	9th	13
5th	16	5th	21		

Elasmosaurid species	Number of symphyseal alveoli	Number of premaxillari alveoli	Number of pre-orbital alveoli in mandible
Leivanectes bernardoi gen. at sp. nov. (FCG-CBP-22)	3	5	7
Eromangasaurus australis (QM F11050)	~5	4 (left)/ 3(right)	7+
Callawayasaurus colombiensis (UCMP 38349, holotype; UCMP 125328 referred)	~5-6	5	~11
Libonectes morgani (SMUSMP 69120)	4	5	10
Thalassomedon hanningtoni (UNSM 50132)	?	5?	~10
Futabasaurus suzukii (NSM PV15025)	~4	5	~12
Zarafasaura oceanis (OCP DEK/GE 315)	~4	4-5	7?
Tuarangisaurus keyesi (NPC CD 425)	4	5	10
Terminonatator ponteixensis(RSM P2414.1)	3	4 left/1midline/4 right	~10
Lagenanectes richterae (BGR Ma 13328)	4	5	8+, *~13*
Styxosaurus browni (AMNH 5835)	?	4-5	9+
Styxosaurus snowii (KUVP 1301)	3	5	8+
Nakonanectes bradti	3	5	~8


A
Bogotá
Loma Puntillas
Q. El Roble
X = 1'120.000
N
Loma La Cabrera
Río Leiva
Monquirá
Río Sutatoca
Loma La Catalina
VILLA DE LEIVA
X = 1'114.000
Y = 1054.000
Y = 1060.000
0
2 Km
B
Albian
Aptian
Barremian
Hauterivian
Grupo de San Gil
Formación Paja
Formación Ritoque
Formación San Gil Superior
Arcillolitas con nódulos huecos
Arcillolitas abigarradas
E
D
C
B
A
Lutitas negras inferiores
FCG-CBP-22
50 m
C
LEGEND
Claystone
Arenaceous claystone
Calcareous claystone
Calcareous arenaceous claystone
Sandstone
Arenaceous limestone
Calcareous concretions


A
pmx
1st
2nd
3rd
de
E
B
pmx
en
mx
prf
f
pof
4th
5th
3rd
2nd
pl
de
C
mx
pl
pt
p
fr
pmx
en
prf
pof
D
a
c
mx
de
sp
v
in
pt
pl


A
100* AMD/preob
14
16
12
10
8
6
4
2
Leivanectes bernardoi nov. gen et sp.
1st
5th
Tuarangisaurus keyesi
5th
Callawayasaurus colombiensis
5th
Tooth position
B
AMD
25
20
15
10
5
Leivanectes bernardoi nov. gen et sp.
5th
1st
Tuarangisaurus keyesi
5th
Callawayasaurus colombiensis
5th
Tooth position
C
10th
20th
D
1st
E
1st
F
10th
G
10th
H
1st